

Review article

Biology of common crupina and yellow starthistle, two Mediterranean winter annual invaders in western North America

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This paper reviews the biology of two closely related Mediterranean annuals, yellow starthistle and common crupina, which have invaded grassland, shrub steppe, and open woodland habitats in western North America. Despite the similarity of their winter annual life cycle, the two species differ significantly in population dynamics. Common crupina has traits that favor persistence rather than rapid population growth: large, heavy achenes with an after-ripening requirement; lower fecundity but higher germination success; and reproduction regulated by vernalization and photoperiod in addition to thermal time. Persistence traits also foster invasion of undisturbed or less degraded steppe habitats. Yellow starthistle has more ruderal traits: small, light, rapidly germinating achenes; higher fecundity, with greater seedling mortality; and reproduction that is less sensitive to photoperiod and vernalization. These characteristics confer a greater adaptability for rapid spread and colonization of disturbance by yellow starthistle than by common crupina. An understanding of the relative differences in biological characters of each species and in their function in invaded environments is relevant to ecological management of these pest species.

Nomenclature: Common crupina, *Crupina vulgaris* Cass., CJNVU; yellow starthistle, *Centaurea solstitialis* L., CENSO.

Key words: Alien plants, biological invasion case study, exotic plant pest.

Various studies have identified traits associated with weeds and invasive species. These studies and the classic lists of Baker (1965, 1974) have had the objective of evaluating the relative threat posed by potential invaders (Venette and Carey 1998; White and Schwarz 1998). Emphasis has centered on prediction, using biological characteristics to distinguish invaders from noninvaders. 'Post-hoc evaluations' of invasions have been criticized as having little predictive value (Beerling 1995). The underappreciated value of biological invasion case studies lies in their application in ecologically based pest management. Schierenbeck (1995) noted that "not until there is a thorough understanding of how each invader functions in its new environment will there be some modicum of control against these pests." Understanding the ecology of invasive species is a vital part of all pest management, which ranges from intensive agricultural weed control to maintenance of native landscapes. Prediction and prevention are essential, but managing the numerous already-entrenched invaders is an even larger responsibility.

Although the practice of grouping species with similar characteristics for common pest management strategies conserves time and money, it should not be assumed that all species in a group are 'ecological equivalents', identical in their response to environmental conditions. Two invaders in the western United States, yellow starthistle and common crupina, are commonly grouped together because they share many similarities as members of closely related genera within the same tribe (Asteraceae: Cynareae). Both species are facultative winter annuals of Mediterranean origin that ger-

minate with autumn rains and that utilize a rosette growth form to exploit favorable microclimatic conditions at the soil surface during the winter (Regehr and Bazzaz 1976). South-facing natural grasslands provide more favorable light and temperature conditions than do other habitats in the Pacific Northwest, and these grasslands are more susceptible to invasion by both species. As mature plants, both species have low palatability to herbivores, with physical defensive traits, including stiff trichomes (common crupina) and sharp spines (yellow starthistle).

The purpose of reviewing both species in one article is to compare and contrast biological characteristics that influence weediness. This approach also allows a more holistic presentation of how traits are integrated within each species and shows where strength in one attribute may compensate for weakness in another. The overall objective is to relate biological traits to species behavior in introduced environments, providing a foundation for improved management of the weed populations.

Overview of Invasion History

Yellow starthistle became established in western North America in the mid-1800s and now infests more than four million hectares (Thomsen et al. 1996), primarily in California, Oregon, Idaho, and Washington. Yellow starthistle infests annual and perennial grasslands, shrub steppe, oak savannas, open woodlands, and modified habitats such as pastures, hayfields, orchards, and vineyards. The first records of yellow starthistle in California are linked with Spanish

colonial activities, as shown by achenes found in adobe bricks of the Mexican period, which began in 1824 (Hendry and Bellue 1936). Most pre-1900 California collections are clustered near alfalfa (*Medicago sativa* L.) production and feeding sites. Between 1850 and 1898, almost all of the imported alfalfa seed planted west of the Rocky Mountains was grown in Chile from seed of Spanish origin starting in the 1600s, but some seed may have come from France (Gerlach 1997). Seeds were also brought in ship ballast to both eastern and western seaports (Howell 1959; Roché and Talbott 1986), but these introductions appear to be relatively unimportant when compared to introduction and spread with alfalfa seed. From 1900 through the 1920s, alfalfa production expanded rapidly, and yellow starthistle was widely distributed in contaminated seed across California, Oregon, Washington, and Idaho (Gerlach 1997; Maddox et al. 1985; Roché 1965; Roché and Talbott 1986). When the demand for alfalfa seed skyrocketed, the United States became a dumping ground for the world's junk seed because it lacked legal protection against imported weed seeds until 1912, thereby allowing suppliers to increase profits by diluting pure seedlots with screenings (Gerlach 1997). Sometime during the 1930s or 1940s, yellow starthistle moved from the alfalfa-cereal grain cropping system to invade the foothill rangelands in California (Gerlach 1997). By the 1970s, yellow starthistle populations in many areas had coalesced to occupy large, contiguous areas in Idaho, Oregon, and Washington, as well as in California, thus intermingling introductions from different sources.

Common crupina was listed as a "Federal Noxious Weed" after its discovery on 18 ha of rangeland in Idaho in 1968 (Stickney 1972). It infests about 20,000 ha of rangeland, primarily canyon or foothill grasslands, but also shrub steppe and open forest types (Thill et al. 1999). It was found in an abandoned field near Santa Rosa in Sonoma County, CA, in 1975 (Davis and Sherman 1991); near Lake Chelan in Chelan County, WA, in 1984; in Umatilla County, OR, in 1987 (Couderc-LeVaillant and Roché 1993); and in two additional locations in California: at Annadel State Park in Sonoma County in 1989 (Davis and Sherman 1991) and near Kelly Springs in Modoc County in 1991 (Couderc-LeVaillant and Roché 1993). The means and source of the initial introduction remain unknown, although multiple introductions are implied by the presence of two apparent varieties, *typica* and *brachypappa* (Couderc-LeVaillant and Roché 1993). Because no common crupina was found in 1958 plant inventories of areas in Idaho that were infested in 1980 (Miller and Thill 1983), its initial introduction appears to have occurred not much more than 40 yr ago, at least 100 yr later than the introduction of yellow starthistle. Although local expansion has occurred, including dispersal to new satellites, major populations of common crupina remain discrete and are widely separated from each other, in contrast to the merging of yellow starthistle populations.

Review of Biology

Phenological Development

In Mediterranean climates and other regions with a summer drought, the timing of reproduction is a critical factor in the competitive ranking among annual species, because

availability of water regulates the amount of seed produced (Hironaka 1990). A common adaptation among Mediterranean annuals is to avoid the summer drought by flowering early and maturing seed before depletion of soil moisture (Dallman 1998).

Differences in reproductive phenology are readily apparent among winter annuals in the canyon and foothill grasslands of north-central Idaho, northeastern Oregon, and eastern Washington (45°50'N to 48°8'N latitude). Downy brome (*Bromus tectorum* L.) flowers earliest, in late April. Common crupina flowers in May, about the time that downy brome seed matures (Miller 1982; Sheley and Larson 1994a). Common crupina achenes mature in June (Miller and Thill 1983; Prather et al. 1991; Sobhian et al. 1996), when yellow starthistle is entering its bud stage. By the time yellow starthistle flowers in July and produces mature seed in August, nearly all of the associated vegetation has long since senesced (Roché 1965; Sheley and Larson 1994a).

The consequences of earlier maturity often include a reduction in plant size and seed production, which results from the short growth period, as seen in common crupina. Conversely, late-flowering species, such as yellow starthistle, attain larger plant size and higher fecundity by growing for a longer period and using more resources, although they risk severe reduction in seed output during drought years.

Thermal time (degree days), photoperiod, and vernalization commonly regulate reproductive phenology in temperate winter annual species. Base temperatures for development were similar in populations of common crupina (ca. 1°C) and yellow starthistle (2°C) from Idaho (Roché et al. 1997a, 1997c). In a study conducted at Moscow, ID (46°44'N latitude), the two species shared two other aspects of reproductive development—delayed development with increased intraspecific competition and synchronization of flowering among fall germinants—but differed in their response to vernalization, photoperiod, and thermal time (Roché 1996).

As a short long day plant sensitive to vernalization, common crupina initiated flowering sooner with cold temperature/short daylength vernalization of seedlings or imbibed seeds, followed by long days (Patterson and Mortenson 1985; Roché et al. 1997b). Yellow starthistle was less sensitive to photoperiod and the absence of cold temperature vernalization did not delay flowering (Roché et al. 1997c). Sobhian (1993) observed normal flowering in nonvernalized yellow starthistle sown in a greenhouse in March and moved to garden plots in May. Differences in thermal time requirements from emergence to selected stages of reproductive development (bud, flower, seed) correspond to phenological differences between the two species observed in natural environments. A population of yellow starthistle from Lewiston, ID (46°30'N latitude), required approximately twice as many degree days for reproduction as Oregon and Idaho populations of common crupina (Table 1) when both were grown in field plots at Moscow, ID. Obviously, these reproductive requirements limit yellow starthistle to warmer climates than common crupina, with major consequences for the potential invasion scope by each species.

Breeding Systems

Yellow starthistle and common crupina share some traits in their pollination biology; both are preferential outcrossers

TABLE 1. Thermal time (degree days C) from emergence to mean first occurrence of three stages of development in common crupina and yellow starthistle. Base temperatures used for calculations were 1 C for common crupina and 2 C for yellow starthistle (Roché 1996).

	Bud stage	Anthesis	Achene dispersal
	degree days		
Common crupina	600	800	1,150
Yellow starthistle	1,240	1,740	2,140

(Couderc-LeVaillant 1984; Maddox et al. 1996) that attract generalist insect pollinators with pollen and nectar (Burgett et al. 1989). Yellow starthistle is predominantly self-incompatible (Harrod and Taylor 1995; Maddox et al. 1996; Sun and Ritland 1998), in contrast to common crupina, which is facultatively autogamous (Couderc-LeVaillant 1984). Stigmas within fertile flowers of common crupina are receptive for 1 d before the corolla withers. When conditions are not favorable for pollinators, selfing becomes the dominant mode of pollination, without notable loss in fecundity (Roché 1996).

Among populations of yellow starthistle from California, Idaho, and Washington, Sun (1997) reported an average population outcrossing rate of 97.5% and about 6% apparent selfing (biparental inbreeding). Sun and Ritland (1998) obtained only three achenes from a single capitulum among 18 that were bagged to exclude pollinators. Although autogamy generally plays an insignificant role in seed production, individuals (Maddox et al. 1996) and populations (Sun and Ritland 1998) vary in self-incompatibility (Table 2). The ability to produce at least a few seeds by pollination within the same capitulum or between capitula on the same plant can be highly significant during colonization events. Higher levels of inbreeding in yellow starthistle populations that are isolated geographically or seasonally indicate that sporophytic incompatibility may fail under some conditions (Sun and Ritland 1998) or may be lower in certain individuals (Maddox et al. 1996). In yellow starthistle, outcrossing is enhanced by spatial and temporal separation of male and female parts within each capitulum (Maddox et al. 1996). In addition, outcrossing is favored by plant-to-plant foraging behavior of European honeybees and by the limited number of capitula available for pollination on individual yellow starthistle plants at any given time (Maddox et al. 1996). Timing of flowering in yellow starthistle, which is later than its associated vegetation, may reduce competition for available pollinators and increase reproductive success (Harrod and Taylor 1995). In California, the introduced European honeybee was responsible for up to 50% of seed set in yellow starthistle, whereas the rest was caused by all other pollinators (Barthell et al. 1994).

Fecundity

The potential for reproductive output is much lower in common crupina than in yellow starthistle, whether this output is measured as number of achenes produced per head, per plant, or per unit area. Involucres of common crupina (7–12 by 14–23 mm) and yellow starthistle (8–12 by 13–16 mm) do not differ greatly in size (Davis 1975;

TABLE 2. Mean number of yellow starthistle achenes produced by different pollination methods.

	Achenes per capitulum	
Autogamy (same capitulum)	10.4 ^a	0.5 ^b
Geitonogamy (same plant)	18.9	
Xenogamy (between plants)	34.6	9.1
Open pollinated (with insects)	56.5	33.1

^a Harrod and Taylor (1995).

^b Maddox et al. (1996).

Hickman 1996) and contain both sterile and fertile florets. The number of fertile florets, which represents the potential achenes per head, are an order of magnitude greater in yellow starthistle than in common crupina.

Fertile florets ranged from one to eight in number, accompanied by three to eight sterile florets in capitula of European populations of common crupina (Couderc-LeVaillant 1984). In an Idaho common crupina population, the most common combination comprised two fertile and three sterile florets (Roché 1996). The first flowering head per plant in the Sonoma County, CA, and the Umatilla County, OR, populations contained an average of 3.5 fertile and five sterile flowers (C. T. Roché, personal observation, 2000). Normally, one or two achenes mature per capitulum (Zamora 1988). Gunn and Faul (1979) described a whorl of about 30 silvery, 11-mm-long smooth bristles within the innermost phyllary bracts that derive from pappus remnants of aborted achenes, and they indicated that commonly only one achene matured. Kambitsch (1983) noted drought-related achene abortion as a factor that limited reproductive output in common crupina.

In addition to sterile and fertile florets, yellow starthistle produces dimorphic achenes. The sterile florets occur in the outermost circle, followed by plumeless achenes in the next ring and plumed achenes in the interior. Roché (1965) found that 21 to 23 peripheral and 70 to 80 interior florets produced a mean of 51 total achenes per capitulum, with a ratio of plumed to plumeless achenes of approximately 3:1 among populations from southeastern Washington. Sun and Ritland (1998) reported a mean of 75 (56 to 100) total florets, which produced an average of 53 achenes per capitulum. Pitcairn et al. (1998) reported a linear relationship between floret number and involucre diameter, with fertile (plumed and plumeless) florets in the same range as previous estimates (Roché 1965; Sun and Ritland 1998), and about 8 to 24 sterile florets per capitulum.

The effect of reproductive fluctuation on number of propagules is profoundly different between yellow starthistle and common crupina. If each doubles the number of achenes per capitulum under favorable conditions, common crupina might increase from one to two achenes, or from two to four achenes, whereas yellow starthistle increases from 30 to 60 achenes per capitulum. This disparity is amplified by differences in the number of capitula per plant.

Among measures of plant size, the number of capitula per plant is the best predictor of reproductive output in yellow starthistle (Pitcairn et al. 1997). Whereas yellow starthistle more typically produces 700 to 10,000 achenes per individual (Maddox 1981), an estimated 105,000 achenes were contained in the 3,400 capitula on an unusually large individual (Thomsen et al. 1996). In studies of reproductive

plasticity relative to density in yellow starthistle, Pitcairn et al. (1997) found that the number of capitula per plant decreased exponentially with increasing density, reaching a "constant final yield" of just over 1,500 capitula m^{-2} for one site and year. As this potential yield varies from year to year and site to site, it indicates the species' capacity to respond to environmental conditions by indeterminate flowering and by aborting immature capitula. In California annual grasslands, yellow starthistle produced 10,000 to 40,000 achenes m^{-2} (Thomsen et al. 1996), whereas annual output in southeastern Washington ranged from 5,200 to 21,600 achenes m^{-2} from a stable adult population of 200 plants m^{-2} (Sheley and Larson 1994a).

Fecundity estimates in common crupina are an order of magnitude smaller. On an Idaho dry grassland site, Zamora (1988) reported a range of 3 to 27 capitula per plant, with a total of only 2.4 to 23 achenes per plant. As an indication of potential response to favorable conditions (i.e., almost unlimited resources), common crupina from Idaho and Oregon grown in experimental farm plots at Moscow, ID, averaged as many as 250 capitula and 800 achenes per plant, and the Washington population produced over 400 capitula and 850 achenes per plant (Roché 1996). Compared to hundreds of plants and tens of thousands of achenes per square meter of yellow starthistle, typical populations of common crupina in natural settings were 50 adult plants m^{-2} (Belles et al. 1981) and 1,000 achenes m^{-2} (Zamora 1988).

Achene Size

Numbers of propagules tell only part of the story, as achenes of common crupina and yellow starthistle differ dramatically in size. But before discussing this, it is necessary to explain the apparent common crupina varieties mentioned earlier. Beauverd (1912) described two subspecies with five varieties of common crupina in central Europe, based on characteristics of the achene (size and length of the achene and color of the pappus), the number of florets, and relative size of the stigma and style. Unfortunately, this classification is based on specimens from a small area (Upper Basin of the Rhone River) at the northern limits of the species range, and considerable variation in achene size and color have been noted not only between populations but also within plants during field collections of achenes across Spain, France, Greece, Italy, and Switzerland (C. T. Roché, personal observation). Based on interpretation by Couderc-LeVaillant (1984), the North American populations were categorized as either variety *typica* or *brachypappa*. Achene size in American populations has been shown to be a reliable character that does not vary with growing conditions. But no systematic evaluation has been done to determine whether greater population level genetic variability occurs in these characters across the native range of the species. Recognizing that the American populations may not be true varieties and that achene size differences could be the result of genetic bottlenecks during transcontinental migration, we will make only limited use of the previous varietal designations. Two populations (Washington and Modoc County, CA) were grouped as variety *brachypappa* based on a smaller achene (19 mg) with a shorter pappus (4–5 mm), and the remaining three populations (Idaho, Oregon, and Sonoma County, CA) were grouped as variety *typica*, with a larger

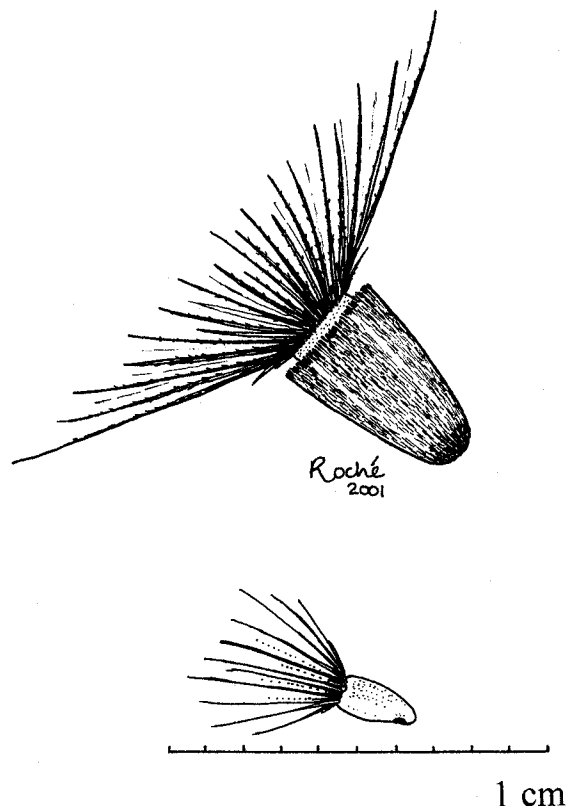


FIGURE 1. Achenes of yellow starthistle (bottom) and common crupina (top), showing relative size and manner in which pappus orients hilum end to soil surface.

achene (4–5 mm long by 3–4 mm wide) and a longer pappus (7–9 mm) and weighing 36 mg (Couderc-LeVaillant and Roché 1993; Gunn and Faul 1979; Reed 1977; Roché 1996).

Plumed achenes of yellow starthistle are about 2 to 2.5 mm long, with a 4-mm pappus, and they weigh about 1.9 mg (Roché 1965). Unplumed achenes (lacking a pappus) are slightly lighter, at 1.4 mg (Roché 1965). Common crupina (var. *typica*) achenes are 2 to 2.5 times longer and 20 times heavier than plumed achenes of yellow starthistle (Figure 1).

Using the values of 2.4 to 23 achenes per plant, common crupina reproductive output ranges from 0.09 to 0.8 g per plant, compared with 1.2 to 17.7 g of achenes per plant in yellow starthistle (700 to 10,000 achenes, assuming a 3:1 ratio of plumed to unplumed achenes). Converting this to the per-area basis described earlier, seed yield mass is much closer: common crupina (1,000 achenes per m^2) with 36 g m^{-2} compared to yellow starthistle (5,200–40,000 achenes per m^2) with 9 to 71 g m^{-2} .

Propagule Dispersal

The mechanism of release of achenes in both species is typical of the Cynareae (Sheldon and Burrows 1973; Zohary 1950). As achenes mature, the receptacle and phyllary bracts dry and contract, forcing the detached achenes up to a free position atop the capitulum, where slight motion of the plant dislodges them. Achenes retained when moisture recloses the phyllary bracts are released upon redrying. Although a plume is widely perceived as a wind dispersal de-

vice, almost one-half of the yellow starthistle plumed achenes fell within 0.3 m of the perimeter of the mother plant, and 92% fell within 0.6 m (Roché 1992). Achenes of common crupina, with an even poorer ratio of pappus size to achene weight than yellow starthistle, also fall relatively close to the source.

The pappus functions primarily to orient the achene for optimum germination success. By means of their weight, shape, and pappus, common crupina achenes filter down through the litter layer to reach mineral soil. Fine hygroscopic bristles located on the pappus pull achenes across the soil surface as the relative humidity fluctuates (Pijl 1969). Upon wetting and redrying, the primary pappus hairs spread horizontally to assume a position perpendicular to the long axis of the achene (Roché 1996). This pappus orientation tips the achene to an angle that positions the hilum, where the radicle protrudes, against the soil surface (Figure 1). It also prevents achenes from slipping too deeply into crevices at the soil surface. Belles et al. (1981) also noted that mature achenes fall to the ground hilum-end first and are buried up to the pappus in light dry soils. Similar penetration of plant residue is attained by plumed achenes of yellow starthistle, whose fall is directed like an arrow so that the tip slides between pieces of litter (Gerlach, pers. comm.). Small barbs on the pappus bristles work the achene to the soil surface as the pappus opens and closes with drying and wetting cycles. In long-distance dispersal, the pappus may aid flotation in moving water or lodge achenes in various surfaces or crevices such as hair, feathers, clothing, tires, and screens (Thomsen et al. 1996).

Vehicles and many other types of equipment also transport seed over long distances. Transport of contaminated soil and gravel has been a major contributor for both species, and as previously noted, contaminated legume seed has been a primary long-distance dispersal route for yellow starthistle. Zamora and Thill (1989) reported rodent transport of common crupina achenes for 15 m, and seedlings are frequently seen clustered, as in rodent caches. All common crupina achenes ingested by pheasants, cattle, horses, sheep, and deer were excreted within 5 d, with subsequent germinability ranging up to 81% in deer (Thill et al. 1986). Although many yellow starthistle achenes are consumed by birds, most are lost to the regeneration pool, because finches hull seeds before ingestion, and pheasants and quail grind them in a gizzard (Roché 1992).

Germination and Seedbank Persistence

After-ripening has been reported to enhance germination in both common crupina and yellow starthistle, but the level of inherent dormancy differs dramatically between species. Germination of fresh achenes of common crupina was very low, less than 5%, and achenes were extremely prone to fungal attack (Roché 1996; Zamora 1988). Achenes dispersed early in the season had the highest level of germination resistance, when delay of emergence would greatly increase the probability of seedling survival (Zamora 1988).

In yellow starthistle, some researchers encountered no dormancy at dispersal time in achenes exposed to light under optimal temperatures in Washington and northern Idaho (Roché 1965, 1996), but researchers in California found a slight increase in germination percentage following an after-ripening period (Joley et al. 1997). In studies conducted

in Placer County, CA, Joley et al. (1992) reported a mean germination of 84% in yellow starthistle achenes 1 wk after harvest in one year but an increase from 67 to 98% germination after 1 mo of dry storage the following year. Joley et al. (1997) concluded that light is required for maximum germination in yellow starthistle and that darkness and temperature extremes hindered germination, whereas alternating temperatures favored it. Unplumed achenes generally had lower germination rates than plumed achenes, especially under dark or cold conditions (Joley et al. 1997). While attributing complex interactions between fluctuations in temperature, light, moisture, achene type, and dispersal date to an ecological cause, they suggested that a low degree of dormancy in freshly matured achenes is relatively unimportant in California, where yellow starthistle germination is synchronized with other winter annuals by summer drought and autumn precipitation. Dormancy related to after-ripening would prevent seedbank depletion by sporadic summer rain events, a more important mechanism in common crupina, whose propagules disperse 1 to 2 mo earlier than those of yellow starthistle. However, some seedlings of common crupina had emerged by late August 1999 in France and Spain, so summer germination is not unknown within the native range of the species (C. T. Roché, personal observation).

With seed production exceeding mature plant stocking levels by a 20- to 100-fold measure, yellow starthistle populations are buffered against predation and potential heavy losses in seedbanks by early rain followed by drought. Overproduction of seeds and "superabundance in the seedbank" are often coupled with lack of dormancy and the ability to germinate at high seedbed temperatures with the first flush of germination (Young and Evans 1989). In Greece, Sobhian (1993) observed yellow starthistle germination in response to a 13-mm rainfall in mid-August; during this period, nearly all of the seedlings subsequently died from drought, and the few survivors grew very large rosettes, a few of which bolted or flowered by late autumn. Although summer precipitation adequate to trigger germination is rare in California, early germination could occur along streams or in response to irrigation and following August thunderstorms in north-central Idaho and eastern Oregon and Washington. Although drought mortality among summer germinants may ravage the cohort, survivors could overwinter as rosette through bud-stage plants. In experimental plantings in Moscow, ID, yellow starthistle died if flowering began before freezing winter temperatures (Roché et al. 1997c).

A more important response to ephemeral summer precipitation, along with dew, lies in the effects of cyclic wetting and drying of achenes lying in the litter or soil surface. In the laboratory, fresh common crupina achenes exposed to a cycle of wetting and drying germinated in higher percentages and did so more quickly than did unprimed achenes at 15 and 20 C (Roché 1996). Under natural conditions, achenes would be exposed to several cycles of wetting and drying by autumn and should germinate more rapidly than achenes stored dry in the laboratory for an equal after-ripening period.

In addition to massive seed production, yellow starthistle has a second survival mechanism, in the form of dimorphic achenes (Roché 1992). Plumeless achenes are retained in the capitula until the involucre bracts fall off during winter,

thus delaying germination for a portion of the propagules. Involucral bracts may prevent precocious germination of plumeless achenes in the capitulum by excluding light or by chemical inhibitors (Joley et al. 1997). A predispersal seedbank investigated in southeastern Washington by Sheley and Larson (1994a) consisted entirely of plumeless achenes, even though plumeless achenes comprised only 25% of the total seed output. Other studies, conducted in California, recovered both types of achenes following rainy season depletion of the seedbank, although sometimes at a higher ratio of plumeless to plumed achenes than in the seed output (Joley 1994; Joley et al. 1992). Interactions between temperature, moisture, and light (quality, quantity, duration) have been shown to influence germination response in yellow starthistle (Joley 1994; Joley et al. 1997; Larson and Kiemnec 1997). The same factors likely interacted for seasonal dormancy that minimized spring emergence in buried achenes of common crupina (Thill et al. 1985).

The complexity of seedbank dynamics is far from fully understood for either species, but neither species appears to depend on large numbers of seed persisting for long periods of time. This behavior is consistent with the low carryover of germinable seeds by other species in annual grasslands, about 1% of annual production (Young and Evans 1989). Bazzaz (1996) noted that most winter annual composites recruit heavily from newly dispersed seed rather than from seedbanks. Most yellow starthistle seed germinates or is lost to predation or decay, with the carryover primarily on the soil surface or in the litter (Joley et al. 1992; Roché 1992). Just before dispersal, a seedbank of yellow starthistle in southeastern Washington contained about 3,000 achenes m^{-2} , representing about 13% of total annual output (Sheley and Larson 1994a). Depletion studies demonstrate the value of annual replenishment of the seedbank. From an initial store of about 4,000 yellow starthistle achenes m^{-2} , only 5.6 and 3.9% remained after 2 and 3 yr, respectively, when seed dispersal was prevented (Joley et al. 1992). Three years of consecutive burning before seed maturity reduced the seedbank of yellow starthistle by over 99% (DiTomaso et al. 1999). Under natural conditions, 90 to 98% of common crupina achenes germinated the first autumn after production, and none were found in the soil seedbank after 4 yr (Zamora and Thill 1989). In both species, buried achenes persisted for longer periods (Callihan et al. 1993; Joley et al. 1985; Thill et al. 1985).

Germination rate and seedling growth are faster in yellow starthistle than in common crupina. At optimum temperatures for germination, radicle protrusion from yellow starthistle achenes begins in 24 h (Roché 1965; Roché et al. 1997c). Common crupina achenes germinated in 5–8 d at the optimum temperature, 10.5 C (Roché 1996). Sheley et al. (1993) reported radicles that were 34 and 32 mm long for plumeless and plumed achenes, respectively, in 96 h at 18 to 20 C. Roché (1965) recorded mean radicle lengths of 71 and 57 mm for plumeless and plumed achenes, respectively, by the time cotyledons had developed, at alternating temperatures of 20 and 30 C. This capacity for rapid germination and establishment allows yellow starthistle to excel in colonizing highly disturbed sites, compared to the slower response of common crupina.

Seedling Establishment

Both common crupina and yellow starthistle germinate following autumn precipitation and grow into rosettes over

the winter, utilizing the warmer microclimate at the soil surface. Moisture is normally ample during winter, but low temperature and light may limit growth. In both annual and perennial plant communities, residual plant debris reduces light at the soil surface. Litter and living cover also improve conditions for seed germination by moderating temperature and moisture fluctuations (Evans and Young 1970). In addition to desiccation, frost heaving causes significant mortality among yellow starthistle seedlings in southeastern Washington (Sheley and Larson 1994a) and southwestern Oregon (G. R. White, personal communication). Associated with fine-textured soils and diurnal subfreezing temperatures, frost heaving has not been noted as a mortality factor farther south in California (J. D. Gerlach, personal communication).

Excessive residual plant litter retards, rather than promotes, seedling establishment. Yellow starthistle is vulnerable to shading, as evidenced by etiolation of seedlings under tall, dense stands of annual grasses, with rosettes having fewer leaves and tending to be upright rather than prostrate (Thomsen et al. 1996). After noting the absence of yellow starthistle on north aspects, Roché (1965) investigated lower levels of light and found that shaded rosettes grew weak and spindly, with erect yellowish-green leaves, compared to vigorous blue-green leaves of prostrate rosettes in full sun. Common crupina also forms a compact rosette in full sun, with numerous leaves near the soil surface. Unlike yellow starthistle, shaded common crupina seedlings elongate a stem between the early leaves, raising them up through the litter layer during the winter for better light exposure (Roché 1996). Energy reserves in large cotyledons allow common crupina to circumvent rosette limitations when seedlings are heavily shaded by plant debris. However, if prevented from reaching adequate light, common crupina seedlings also become etiolated (Roché 1996). Surviving yellow starthistle rosettes have been observed growing up through the litter layer by April in California (J. D. Gerlach, personal communication).

The pattern of winter root growth and its response to shade is similar for common crupina and yellow starthistle (Roché 1996). First, a primary taproot achieves rooting depth and then is supplemented by shorter secondary branches (Roché et al. 1994). During the period of short days and colder temperatures of early to mid-winter, roots grow relatively slowly, and plants develop few leaves. Following a planting date of November 6 in the Snake River Canyon in southeastern Washington (46°20'N latitude, 364-m elevation), roots of common crupina and yellow starthistle grew less than 0.5 $cm d^{-1}$ until late February. Then the growth rate increased to 1 to 2 $cm d^{-1}$ for plants in full sun but remained less than 0.8 $cm d^{-1}$ for plants shaded by a litter cover (Roché 1996). Other studies of yellow starthistle seedling root growth recorded 1.7 $cm d^{-1}$ at greenhouse temperatures of 20/15 C (Sheley et al. 1993) and 0.9 to 3.7 $cm d^{-1}$ in a growth chamber at 10 C (Sheley and Larson 1994b). Under full sun winter field conditions in Pullman, WA (46°44'N latitude, 750 m elevation), yellow starthistle roots grew 0.2 to 0.7 $cm d^{-1}$ from November through February and then grew 1 to 2 $cm d^{-1}$ in March and April (Roché et al. 1994). Root growth dropped to half that rate among plants intercepting 80 to 90% less sunlight (Roché et al. 1994).

As facultative winter annuals, both species continue to recruit seedlings throughout the winter into early spring. However, seedling numbers and mortality in yellow starthistle far exceed those in common crupina. Sheley and Larson (1994a) reported 4,000 yellow starthistle seedlings m^{-2} in mid-November, adding about 1,000 individuals per week for 6 wk, peaking in late January at 7,600 seedlings, and declining to 4,700 seedlings m^{-2} by mid-March. Fewer than 25% of the juveniles survived, and only 25% of the adults reproduced (Sheley and Larson 1994a). Yellow starthistle density in April, which ranged from 40 to 1,020 plants m^{-2} , dropped to 7 to 296 m^{-2} , representing mortality rates from 30 to 82% (Roché et al. 1994). In contrast, common crupina seedling densities averaged 160 to 360 m^{-2} (Zamora 1988). Abundant seed production with high germination and subsequent high mortality in yellow starthistle provides a potential venue for selection of adapted biotypes or, conversely, maintains a diversity within the population that buffers against fluctuating conditions. Lower fecundity and mortality rates may translate to less potential for postinvasion evolution in common crupina.

Ecological Implications

Although yellow starthistle and common crupina share many characteristics, the way in which these are combined results in quite different life strategies. Yellow starthistle is a generalist with more "r" characteristics (smaller, rapidly germinating achenes; higher fecundity, with greater mortality; less sensitivity to photoperiod and vernalization), whereas common crupina exhibits more "K" characteristics (large, dormant achenes; lower fecundity but higher germination success; regulation of reproduction by vernalization and photoperiod in addition to thermal time). Yellow starthistle's success as a ruderal plant is fostered by rapid germination and seedling growth and by overproduction of small, easily dispersed achenes that buffer against heavy mortality among achenes and seedlings. The large cushion for seed and seedling mortality combined with low sensitivity to vernalization and day length indicates a greater adaptability to disturbance in yellow starthistle. Common crupina responds less aggressively to disturbance, which is consistent with its lower intrinsic rate of population increase. Ruderal behavior in yellow starthistle indicates a greater potential for replacement by perennial vegetation, whereas common crupina would persist (albeit in low numbers) in stable communities, which is the pattern observed in southern Europe (C. T. Roché, personal observation).

A few traits of common crupina confer invasive advantages over those of yellow starthistle. An isolated colonizing individual of common crupina retains greater reproductive potential than yellow starthistle. Common crupina seedlings escape shading better than yellow starthistle seedlings by bypassing the ground-hugging rosette stage. Although achenes of both species work down through plant residue to contact mineral soil, the more robust seedlings of common crupina tap larger energy reserves in fleshy cotyledons to grow through the litter layer into sunlight without severely weakening the plant. These traits may contribute to invasion success by common crupina in less disturbed or degraded environments, such as native bunchgrass steppes. They may also explain how common crupina persists in degraded com-

munities, such as annual grasslands, after the cessation of disturbance.

Sun (1997) reported high levels of genetic variation in yellow starthistle in North America. She attributes yellow starthistle's wide ecological amplitude at least in part to this diversity, stating that the "general purpose" genotype (Baker 1965) does not exist in colonial populations of yellow starthistle. Genetic bottlenecks were apparently avoided during colonization by large numbers of seeds in human-mediated migration (Sun 1997; Sun and Ritland 1998). The invasion genetics of common crupina have not been similarly studied, but a much higher degree of bottlenecking is suspected because of this plant's larger propagule size and greater self-fertility. The large achenes of common crupina are more easily removed during seed cleaning processes and are less likely to be transported long distances on surface carriers such as animal coats, radiator screens, or tires. As a consequence of smaller, more numerous propagules, yellow starthistle has dispersed more rapidly, both by natural means and with human agricultural and transportation activities.

As a result, at least in part, of its longer invasion history and wider distribution, more is known about the ecological amplitude of yellow starthistle than about common crupina. The substantially greater thermal time requirement for reproduction in yellow starthistle limits its invasion to warmer climates or microclimates. Extensively distributed in California, yellow starthistle appears to approach its northern limits for North America at 48°45'N latitude in northeastern Washington (Roché et al. 1994). Almost 100 yr after its introduction, over 90% of the yellow starthistle in Washington state (Roché and Roché 1988) infests the warmer natural grassland zones of *Agropyron-Poa* and *Agropyron-Festuca* (Daubenmire 1970) in the canyons of the Snake River and the foothills of its tributaries. Near the periphery of a species' range, limiting factors are more easily identified. For yellow starthistle, the critical requirements appear to be light and warmer temperatures for winter root growth and soil moisture for reproduction during the summer drought period (Roché et al. 1994). Farther north, where temperatures are cooler and precipitation is higher, yellow starthistle grows almost exclusively on steep south-facing slopes of natural grasslands (Roché and Roché 1988; Talbott 1987), implicating the importance of winter insolation. These factors likely limit northern expansion in Europe, where yellow starthistle is listed among unsuccessful invaders in the Czech Republic (Pyšek et al. 1995) and Romania (Prodan 1930).

Maturity date and fecundity were cited as driving factors in a replacement series among annuals in the Pacific Northwest proposed by Hironaka (1990). In his successional progression, winter annuals replace summer annuals [e.g., Russian thistle (*Salsola iberica*) yields to downy brome], and among winter annuals, later maturing species replace the early ones [e.g., downy brome yields to medusahead (*Taeniatherum caput-medusae* (L.) Nevski) or yellow starthistle]. In this scenario, yellow starthistle invades sites dominated by early-maturing exotic annual grasses through utilization of deep soil moisture to produce large numbers of propagules late in the season (Borman et al. 1990, 1991). Plant stature also influences competitive relationships, as taller species like yellow starthistle dominate on sites with adequate soil moisture by shading shorter growing species.

Earlier maturity gives common crupina the advantage in

cooler environments, on shallow soils, and in drought years. Later maturity and larger size translate to a competitive advantage for yellow starthistle in warmer climates, on deeper soils, and in years of greater spring precipitation. Thus, where the invasion amplitude of the two species overlaps, relative population dominance between them can fluctuate temporally or spatially (e.g., common crupina favored by drought years or on shallow soils).

The invasion success of common crupina and yellow starthistle can be interpreted to result from biological traits interacting with different environments. Understanding how each species functions in a new environment furnishes the foundation for the development of ecologically based management for each species across the range of its invasion.

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